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# Sex allocation in the sexually monomorphic fairy martin

Michael J. L. Magrath, David J. Green and Jan Komdeur

Magrath, M. J. L., Green, D. J. and Komdeur, J. 2002. Sex allocation in the sexually monomorphic fairy martin. – J. Avian Biol. 33: 260–268.

Offspring sex ratios were examined at the population and family level in the sexually monomorphic, socially monogamous fairy martin *Petrochelidon ariel* at five colony sites over a 4-year period (1993–1996). The sex of 465 nestlings from 169 broods was determined using sex-specific PCR at the CHD locus. In accordance with predicted sex allocation patterns, population sex ratios at hatching and fledging did not differ from parity in any year and the variance in brood sex ratios did not deviate from the binomial distribution. Further, brood sex ratio did not vary with hatching date during the season, brood number, brood size or colony size. The sex ratio of broods with extra-pair young did not differ from those without, while the sex ratio of broods fathered by males that gained extra-pair fertilizations did not differ from broods fathered by other males. Extra-pair chicks were as likely to be male as female. Neither the total number of feeding visits to the brood nor the relative feeding contribution by the sexes varied significantly with brood sex ratio. Brood sex ratios were also unrelated to paternal size, condition and breeding experience or maternal condition and breeding experience. However, contrary to our prediction, brood sex ratio was negatively correlated with maternal size. Generally, these results were consistent with our expectations that brood sex ratios would not vary with environmental factors or parental characteristics, and would not influence the level of parental provisioning. However, the finding that females with longer tarsi produced an excess of daughters is difficult to reconcile with our current understanding of fairy martin life history and breeding ecology.

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According to sex-allocation theory, parents should produce equal numbers of sons and daughters unless the costs or subsequent fitness returns of the sexes are different (Fisher 1930, Hamilton 1967, Trivers and Willard 1973, Charnov 1982). Among birds, departures from parity of offspring sex ratios have been reported in a broad range of taxa (reviewed in Oddie 1998, Sheldon 1998, Komdeur and Pen 2002), and are perhaps less uncommon than previously thought (Williams 1979, Clutton-Brock 1986). Such skewed sex ratios may result from either differential mortality of young between fertilization and independence or, more controversially, adjustment of the primary sex ratio (Krackow 1995). In birds, equal primary sex ratios are expected to result from the Mendelian process of meiotic segregation (Williams 1979), so departures from parity at the pri-

mary level would have to result from the biased production of gametes at meiosis or selective absorption or dumping of ova, and such mechanisms have yet to be identified (Krackow 1995, Emlen 1997, Sheldon 1998, Komdeur et al. 2002).

A number of studies that reveal offspring sex-ratio biases also propose adaptive benefits to skewed sex ratios, usually where the offspring of one sex are shown or predicted to be more profitable than the other under particular ecological or social circumstances. For example, systematic seasonal variation in raptor fledging sex ratios have been attributed to differences in maturation time of the sexes, one sex having a greater advantage than the other when reared early in the season (Dijkstra et al. 1990, Daan et al. 1996, Smallwood and Smallwood 1998, Pen et al. 1999). Greater variance in the reproduc-

tive value of one sex should also promote adaptive sex-ratio modification in relation to parental and environmental characteristics (Trivers and Willard 1973). For example, sex-ratio variation in birds has been shown to correlate with maternal age, size, condition or social status (e.g. Blank and Nolan 1983, Olsen and Cockburn 1991, Bolton et al. 1992, Wiebe and Bortolotti 1992, Nishiumi 1998, Nager et al. 1999, Heg et al. 2000, Whittingham and Dunn 2000), paternal size, attractiveness or quality (Burley 1986, Ellegren et al. 1996, Sheldon and Ellegren 1996, Svensson and Nilsson 1996, Kölliker et al. 1999, Sheldon et al. 1999), and availability of food (Appleby et al. 1997, Kilner 1998). Differences in the propensity of young to disperse from the natal territory (promoting sex-specific local resource or mate competition) or help at the nest (promoting sex-specific local resource enhancement) have also been linked or shown to influence offspring sex ratios (Gowaty and Lennartz 1985, Ligon and Ligon 1990, Komdeur et al. 1997, Komdeur 1998, Pen and Weissing 2000).

A disparity between the cost of producing one sex over the other is also predicted to result in sex ratios skewed towards the cheaper sex at independence (Fisher 1930). Biased fledging sex ratios towards the cheaper sex have been revealed in some sexually size dimorphic species (review in Pen et al. 2000), though few studies have shown this bias to be evident from hatching (but see Torres and Drummond 1999). Moreover, in some cases biased fledging ratios may arise, non-adaptively, from higher mortality rates among the expensive sex, especially when food is scarce (Clutton-Brock et al. 1985, Teather and Weatherhead 1989, Dijkstra et al. 1998, but see Oddie 2000).

Sex-biased parental care has been revealed in a range of species, where one or both parents preferentially provision one sex (Stamps 1990, Lessells 1998). This has been shown commonly in sexually size-dimorphic species in which the food requirements of the sexes differ (reviews in Anderson et al. 1993, Krijgsveld et al. 1998), but also in monomorphic species (Stamps et al. 1987, Gowaty and Droge 1991). Biased provisioning in species without strong sexual size dimorphism has generally been suggested to result from different degrees of philopatry between the sexes, leading to differences in the potential for local resource or mate competition in the future (e.g. Gowaty and Droge 1991, Hartley et al. 1999).

In most of these scenarios, skewed production or provisioning of the sexes was forecast because of predicted variation in the profitability to parents of producing sons and daughters. In many birds, however, there may be little advantage to be gained from biasing the offspring sex ratio. In sexually monomorphic, socially monogamous species with low rates of extra-pair fertilizations, selection for mechanisms that promote sex-ratio modification may be negligible. Until recently, it has been difficult to assess the sex ratio of nestling birds,

particularly in sexually monomorphic species, because of the difficulty in distinguishing the sexes. New molecular techniques for sexing birds (e.g. Griffiths et al. 1996, 1998), using very small blood samples, now permit identification of sex from the embryonic stage onwards. Perhaps unsurprisingly, most studies to apply these new techniques have investigated species where skewed sex ratios may be anticipated, leading to a bias in the taxa being investigated and most likely a bias towards the reporting of positive results (Festa-Bianchet 1996, Bensch 1999, Krackow 1999, Lessells and Quinn 1999).

In this study we investigate offspring sex ratios in the fairy martin *Petrochelidon ariel*, a small (ca. 11 g), insectivorous passerine endemic to Australia (Turner and Rose 1989). There are a number of reasons why systematic sex-ratio variation at the population or family level is not anticipated in this species. First, adult males and females are similar in size, mass and plumage (Magrath 1999), so the costs of raising sons and daughters are not expected to differ. Further, sex-specific costs associated with local resource or mate competition are unlikely as the proportion of fledglings that return to their natal colony is less than 5%, while only 20% of breeding adults return to the study area in the following year (Magrath 1999). Second, fairy martins breed as socially monogamous pairs and the two sexes were found to have similar means and variances in annual production of fledglings (Magrath 1999). Some males gained extra-pair paternity (14% of 207 chicks were sired by extra-pair males; Magrath and Elgar 1997). However, this did not significantly increase variance in male reproductive success, though our sample of males that sired extra-pair young was small ( $n = 5$ ; Magrath 1998). Similar variances of the sexes in lifetime reproductive success would suggest that parental characteristics are not expected to relate to brood sex ratio. Third, both males and females are equally likely to breed in their first year and there is no evidence that hatching date influences the probability that fledglings, of either sex, return to the study area (Magrath 1999). Consequently, seasonal variation in brood sex ratio is not anticipated.

In this paper we test this prediction that brood sex ratio does not vary systematically with either environmental or parental characteristics in this sexually monomorphic species, and also examine the assumption that parental provisioning is unrelated to brood sex ratio.

## Materials and methods

### Study population

The study was conducted at five naturally occurring colony sites of fairy martins in the Yarra Valley near Melbourne, Australia between 1993 and 1996 (12 colony years). In this population, nesting occurred quite

asynchronously between September and January (Magrath 1999). Colonies ranged in size from 8 to 30 pairs and the sites were spatially separated by at least 500 m. Birds were trapped before dawn in their nests where both parents usually reside overnight. Adult females were distinguished from males by the presence of a brood patch that they acquire for the duration of the breeding season. For most adults, right tarsus length and head-bill length were measured to the nearest 0.1 mm with calipers and body mass measured to the nearest 0.1 g with a Pesola balance. For analysis, we used tarsus length as a measure of adult size because tarsal size generally provides a reliable estimate of body size in passerine birds (Hailman 1986) and was also correlated with the other skeletal character that we measured, head-bill length ( $r = 0.18$ ,  $n = 183$ ,  $P < 0.01$ ). An estimate of body condition was derived for each sex by calculating the residuals from a regression of body mass on tarsus length (see Packard and Boardman 1987).

Since few nestlings returned to breed in the study area, the actual age of most adult birds was unknown. However, as about 20% of adults returned between years, it was possible to classify birds as either with or without known previous breeding experience. On average, birds with previous known breeding experience should also be older. These categories only represent a crude distinction because many of the birds classified as without previous experience may in fact have bred previously at other sites, or not have been trapped in previous years. Consequently, comparisons between birds in these categories represent conservative tests.

The contents of most nests were examined every second day by way of an opening constructed in the side of the nest. Nestlings were removed through this side entrance when 11–17 days old for banding, bleeding and weighing. Clutch size was defined as the maximum number of eggs present in the nest during incubation and classified, for analysis, as either small (2–3 eggs) or large (4–5 eggs). Brood size was defined as the number of chicks present in the nest on day 10 and categorized for analysis as 1, 2, 3 or 4+ chicks. The age of the brood was defined as the number of days from when the first eggs hatched; all chicks in most broods hatch within 24 h. Colony size was estimated as the maximum number of simultaneously active nests present at that site during the course of the breeding season. About 30% of pairs raised two successful broods in the one season, and we defined these as first and second broods for analysis.

### Molecular sexing and parentage analysis

Blood samples of about 50  $\mu$ l were collected from chicks, usually between 12 and 14 days after hatching. Samples were stored at 4°C in 1.5 ml of lysis buffer (0.1

M Tris-HCl, pH 8.0; 0.1 M EDTA, pH 7.4; 10 mM NaCl; 0.5% SDS). DNA was isolated using a standard high NaCl-ethanol extraction procedure (Bruford et al. 1992). Individuals were subsequently sexed using a PCR-based sexing technique involving amplification of variable-sized products from the CHD locus, a gene found on both sex chromosomes (Griffiths et al. 1998). The sex of individuals from ten adult pairs was correctly assigned using this technique, so we could be confident the method worked successfully in this species.

Parentage testing was performed using three hyper-variable microsatellite markers (HrU5, HrU6, HrU7), first identified in the congeneric barn swallow *Hirundo rustica* (Ellegren 1992, Primmer et al. 1995). The DNA genotyping procedure followed Primmer et al. (1995). Chicks were assigned as extra-pair if at least two of their three markers were inconsistent with the putative parental genotypes. The three markers provided an average exclusion probability of greater than 0.99 in this population of fairy martins. Males were assigned as extra-pair fathers if they possessed all three paternally inherited alleles of an extra-pair chick. There was never more than one male from the population that matched all three of an extra-pair chick's paternally inherited alleles.

### Monitoring nestling feeding behaviour

Parental care data were collected using a remote-monitoring system that allows detection and identification of individuals as they arrive at and depart from their nest. Birds were detected using infra-red sensors and identified by transponders (Trovan, 11 mm  $\times$  2 mm) that were attached to the leg bands of most individuals in the study colonies. Detection and identification occurred in the tube-shaped entrance to the nest. Further details on the configuration and reliability of this monitoring system are provided in Magrath and Elgar (1997).

Brood-feeding rate generally reached a plateau between days eight and sixteen of the nestling period (Magrath 1998). Mean brood-visit rate (visits/h) was derived for each bird of pairs that were monitored for at least 25 day-light hours during this 8- to 16-day period. Video observations indicate that food items were delivered to the brood on almost all nest visits by parents during this period.

### Statistical analysis

We used binomial tests to check for departures from equal sex ratios. Other analyses were carried out with a statistical modelling approach using Genstat 5.4.1 for Windows (Genstat 5 Committee 1997). Some data were

potentially non-independent because individual females were represented between one and three times. To account for repeated sampling with an unbalanced design, mixed models were fitted incorporating 'female' as a random factor in addition to the fixed effects of interest.

#### *(a) Factors affecting brood sex ratios*

Variation in sex ratios was examined by defining brood sex ratio as the binomial response variable (number of males over brood size) in a generalised linear mixed model with a binomial error distribution (Genstat 5 Committee 1997). Estimates of the variance components were initially obtained using the restricted maximum likelihood procedure. As the standard errors of the estimates for the random term were found to be large compared to the estimates, indicating negligible dependency associated with 'female', the models were simplified by omitting the random term and using a generalised linear model. Fixed effects examined included environmental and brood effects (colony size, year, hatch date, first or second brood, clutch size and brood size), parental characteristics (male and female breeding experience, male and female tarsus length, male and female body condition), and paternity effects (male was cuckolded, male gained extra-pair paternity). We initially examined environmental and brood effects on sex-ratio variation since data on parental characteristics and paternity effects were not available for some broods. We subsequently examined the effect of parental characteristics and paternity on brood sex ratios controlling for any significant environmental and brood effects or significant interaction terms. At each stage of the analysis we progressively eliminated non-significant interaction terms and then non-significant main effects until only significant effects remained. The significance of fixed effects was assessed using the change in deviance (which approximates to a chi-square distribution) associated with dropping that term from a fuller model. Models drew on sex ratio data from a total of 130 broods, but sample sizes varied depending on the fixed effect examined because data for some variables were incomplete. Broods ( $n = 39$ ) where brood reduction occurred before blood samples could be obtained were excluded since preliminary analyses suggested that brood reduction may alter brood sex ratios (see Results). Restricting analyses further so that the models only included the 84 broods where the entire clutch was sexed does not alter any of the results presented in this paper.

#### *(b) Factors affecting brood provisioning*

Separate linear mixed models were fitted to examine (i) the total number of feeds delivered to a brood, and (ii) the proportion of food deliveries performed

by the male. The REML procedure in Genstat 5.4.1 (Genstat 5 Committee 1997) was used to estimate fixed effects and variance components for the random term 'female'. The deviance explained by a full model was contrasted with that of a sub-model excluding the fixed effect of interest, and the change in deviance was used to assess the significance of terms (Genstat 5 Committee 1997). Variables of interest included environmental and brood effects (year, hatch date, first or second brood, brood size, and the sex ratio of the brood), and parental characteristics (male and female breeding experience, male and female tarsus length, male and female condition). Models initially examined environmental and brood effects on variation in provisioning rate because data on parental characteristics were not available for some broods. We subsequently examined the effect of parental characteristics controlling for any significant environmental and brood effects or significant interaction terms. Sample sizes varied slightly depending on the fixed effect examined because data for some variables were incomplete.

## **Results**

### **Population sex-ratio variation**

A total of 465 chicks were sexed from 169 broods produced by 135 different females. Overall, 51.8% of these chicks were male which does not differ from parity (binomial test  $P > 0.2$ ). Given our sample of 465 chicks we would have detected a significant sex ratio bias if 54.8% had been of the same sex. In the 84 broods where the entire clutch was sexed, 50.3% of 294 chicks were male (binomial test  $P > 0.5$ ) and the mean brood sex ratio was  $0.50 \pm 0.24$  s.d.. The variance in brood sex ratios did not deviate from that expected from a binomial distribution (deviance in null model = 76.3,  $df = 83$ ,  $P = 0.69$ ).

### **Differential mortality of embryos and chicks**

There was no difference in the sex ratio of broods where all eggs were sexed compared with broods where one or more eggs failed to hatch, but no brood reduction took place prior to sexing ( $0.50 \pm 0.03$  s.e. ( $n = 84$ ) and  $0.52 \pm 0.06$  s.e. ( $n = 39$ ) for clutches without and with unhatched eggs, respectively: GLM change in deviance = 0.0,  $df = 1$ ,  $P = 1.0$ ).

Broods that suffered partial brood loss between hatching and banding tended to have a higher sex ratio than broods that did not ( $0.62 \pm 0.09$  s.e. ( $n = 25$ ) and  $0.50 \pm 0.03$  s.e. ( $n = 130$ ), for broods with and without brood reduction, respectively: GLM, change in deviance = 3.2,  $df = 1$ ,  $P = 0.07$ ).

Table 1. Summary of generalised linear models examining brood sex-ratio variation in fairy martins. Model 1 examines brood sex-ratio variation in relation to (a) brood and environmental variables, (b) parental characteristics and (c) paternity effects. Terms included in final model: (a) none, (b) female tarsus length, (c) female tarsus length.

Model 1 – Effects on brood sex-ratio variation	Term dropped	$\chi^2$	df	P
(a) Environmental and brood effects (n = 130 broods)	hatch date	1.2	1	0.27
	first or second brood	2.7	1	0.10
	year	4.3	3	0.23
	clutch size (2/3–4/5)	0.0	1	1.00
	brood size	0.9	3	0.83
	colony size	0.0	1	1.00
(b) Parental characteristics (n = 56–61 broods)	female tarsus length	9.3	1	0.002
	female experience	0.05	1	0.52
	female condition	0.31	1	0.58
	male experience	0.15	1	0.70
	male tarsus length	0.23	1	0.63
	male condition	0.43	1	0.51
(c) Paternity effects (n = 29 broods)	male cuckolded	0.06	1	0.81
	male gains extra-pair paternity	1.16	1	0.28

### Environmental and brood-size effects

Brood sex ratio did not vary significantly between years or between colonies (Table 1). There was also no evidence of systematic seasonal variation in brood sex ratios or for a disparity between the sex ratio of first and second broods of the season (Table 1). Brood sex ratios were also unrelated to clutch and brood size and were not correlated with colony size (Table 1).

### Parental characteristics

There was a negative correlation between brood sex ratio and maternal size (i.e. females with longer tarsi produced a preponderance of daughters) (Table 1; Fig. 1). However, brood sex ratio did not vary with our other measured parental characteristics including maternal condition, maternal breeding experience, paternal tarsus length, paternal condition or paternal breeding experience (Table 1).

The mean sex ratio of broods with at least one extra-pair chick did not differ from those where the social partner gained complete paternity (Table 1). Moreover, there was no difference in the sex ratio of broods sired by males that were successful at gaining extra-pair paternity compared to the broods of males that were not (Table 1). Finally, there was no difference between the number of extra-pair young that were male (n = 11) and female (n = 11).

### Parental care and brood sex ratio

Unsurprisingly, total feeding rate of the brood was strongly correlated with brood size (Table 2). However, there was no relationship between total feed rate and brood sex ratio or any of the other environmental factors or parental characteristics that were included in

model 2 (Table 2). Consistent with this finding, there was no significant difference in the mean mass of male and female nestlings, within mixed sex broods, on the day when chicks were weighed (mean mass difference =  $0.006 \text{ g} \pm 0.10 \text{ s.e.}$ ; paired t-test:  $t = 0.06$ ,  $n = 104$  broods,  $P = 0.95$ ).

The relative feeding contribution by the male increased over the course of the season (from 47% for broods hatching in late October to 55% for broods hatching in mid-January). Relative male contribution was also greater when he was paired with a large female (Table 2; Fig. 2). The relative contribution by the

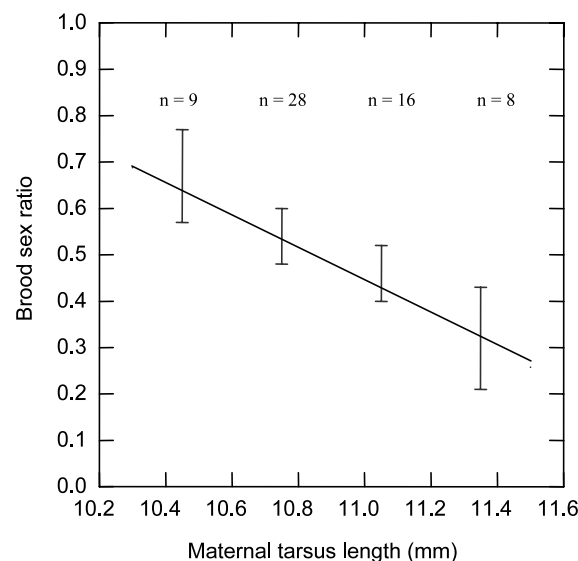


Fig. 1. Brood sex ratio in relation to maternal tarsus length in the fairy martin. Line shows predicted brood sex ratio in relation to female tarsus length as derived from general linear model ( $\chi^2 = 9.3$ ,  $df = 1$ ,  $P = 0.002$ ; Table 1). Vertical lines depict standard error around mean brood sex ratio for females in four categories of tarsus length. N values refer to number of females in each category.

Table 2. Summaries of analyses examining brood provisioning rates of fairy martin pairs using the REML modelling procedure in GENSTAT. Model 2 details how total feeding rate was affected by (a) brood and environmental variables and (b) parental characteristics. Model 3 describes how the relative contribution to feeding by the sexes was affected by (a) brood and environmental variables and (b) parental characteristics. 'Female' was included as a random term in each model. Terms included in final model: (2a) brood size (2b) brood size (3a) hatch date (3b) hatch date and female tarsus length.

Models 2 and 3	Term dropped	$\chi^2$	df	P
2. Total feeding rate (feeds/h)	brood size	52.6	3	<0.0001
(a) Environmental and brood effects (n = 54 broods)	proportion fertile females	1.1	1	0.29
	year	2.2	1	0.14
	hatch date	0.02	1	0.89
	first or second brood	0.0	1	1.00
	sex ratio of brood	1.4	1	0.24
(b) Parental characteristics (n = 41–54 broods)	female breeding experience	0.05	1	0.82
	female tarsus length	0.96	1	0.33
	female condition	0.19	1	0.66
	male breeding experience	1.85	1	0.17
	male tarsus length	0.24	1	0.62
	male condition	0.38	1	0.54
3. Proportion of food deliveries by male	hatch date	5.5	1	0.02
(a) Environmental and brood effects (n = 54 broods)	proportion fertile females	2.04	1	0.15
	year	0.38	1	0.54
	first or second brood	1.45	1	0.23
	brood size	2.27	3	0.52
	sex ratio of brood	0.01	1	0.92
(b) Parental characteristics (n = 41–54 broods)	female tarsus length	9.59	1	0.002
	female experience	0.37	1	0.54
	female condition	0.5	1	0.48
	male experience	0.05	1	0.82
	male tarsus length	1.13	1	0.77
	male condition	2.1	1	0.15

parents, however, was unrelated to the sex ratio of their brood (Table 2).

## Discussion

### Sex-ratio variation in fairy martins

The population sex ratio of fairy martin broods was not different from parity and did not differ between the four years of this study. Furthermore, variation in brood sex ratio did not deviate from the binomial distribution. These observations are consistent with the idea that the profitability of raising sons and daughters does not vary predictably in this species. Furthermore, the sexes appear to be equally costly to produce because (i) they have similar mass at fledging, (ii) food provisioning rate by parents was unrelated to brood sex ratio, and (iii) clutch and brood size was independent of brood sex ratio.

We found no effect of hatching date on brood sex ratio, nor was there a difference in the sex ratio of first and second broods produced during the season. This finding supports the absence of sex-related differences in the possible benefits of hatching early in the season. Indeed, the lack of a correlation between hatching date and likelihood of return in the following season (Magrath 1999) suggests that there may not even be a general recruitment advantage to hatching earlier,

though the sample size of first-year recruits was small (n = 12). Furthermore, the lack of a seasonal change in sex ratio is another indication that the cost of producing sons and daughters is similar. We believe that food availability declines predictably near the end of the breeding season because fledglings are lighter and broods are more likely to be abandoned late in the breeding season (Magrath 1999).

Skewed fledgling sex ratios may nevertheless arise because of differential mortality of either embryos prior to hatching or chicks prior to fledging. We found no evidence for differential mortality of embryos, though there was a tendency for broods that lost chicks before their sex was determined to be more male-biased than broods that did not suffer reduction. We were not able to assess the cause of this apparent bias directly, but such a pattern could arise through either (i) female-biased mortality or (ii) a higher rate of mortality in male-biased broods, independent of sex. One hypothesis that predicts female-biased mortality, even among sexually monomorphic chicks, suggests that harmful mutations should be more commonly expressed in the heterogametic sex (females in birds) (Clutton-Brock et al. 1985, Pen et al. 2000). Females may also be more susceptible to brood reduction if they compete less well (e.g. Oddie 2000) or tend to hatch from last laid eggs. Data to investigate these possibilities were not collected in this study. Higher rates of reduction in male-biased broods could result if male-biased broods required

more food or were produced by parents less capable of provisioning. These possibilities seem unlikely since the sexes appear to be equally costly to raise (see above).

### Parental size and sex ratios

Somewhat surprisingly, we found a strong association between maternal size and brood sex ratio; females with long tarsi produced an excess of daughters while females with small tarsi produced an excess of sons. This relationship was apparently not explained by larger females being in better (or worse) condition than smaller females, as there was no relationship between our estimate of female condition and brood sex ratio. We did not determine if tarsus length was heritable in fairy martins, but it has been shown for a number of species, including the barn swallow that tarsus length has both a paternally and maternally inherited component (Birkhead and Møller 1992). This implies a greater advantage to females than males of large size or conversely a greater advantage to males than females of small size, assuming this relationship has some adaptive benefit. In the American kestrel *Falco sparverius*, larger females also tended to produce daughters (Wiebe and Bortolotti 1992). These authors suggest that larger females may be more effective at incubation, while size in males may be neutral because it does not appear to affect a male kestrel's chance of obtaining a territory or breeding successfully. Larger female size in raptors has

also been suggested to give females an advantage in obtaining mates (Olsen and Cockburn 1991).

We were, however, unable to find any evidence that an increase in size confers a reproductive benefit to female fairy martins. Female tarsus length was unrelated to the date first clutches were initiated, average clutch size, hatching success, the number of broods raised per season, annual production of fledglings, or the probability of returning to the study area (linear or logistic regression analyses;  $n > 60$  and  $P > 0.25$  for all). Female tarsus length was, however, negatively correlated with the proportion of feeding visits females made to the nest (see Fig. 2 and Table 1). One explanation for these patterns is that large size compromises foraging effectiveness, as larger birds may be less agile. This argument has been advanced to explain smaller male size (relative to the female) in many raptor species (reviewed in Andersson 1994). Furthermore, we found negative assortative pairing with regard to tarsus length ( $r = -0.235$ ,  $P = 0.026$ ,  $n = 90$  pairs). This implies that shortfalls in food provisioning by large females may be compensated for by their partner. Possibly, larger females are perceived as more attractive or of higher quality, hence their partners are prepared to invest more in care (Burley 1988). Nevertheless, large size would not be perceived as attractive unless it conveys some benefit, and we could not reveal such an advantage for larger females from our data.

We were also unable to find any evidence that male fairy martins obtain a fitness benefit from being small or suffer a cost when large. Male tarsus length was unrelated to hatching success, the number of broods raised per season, annual production of fledglings, or the probability of returning to the study area (logistic regression;  $n > 60$  and  $P > 0.25$  for all). However, male fairy martins may benefit from being large as males that gained extra-pair fertilizations were both larger than the male they cuckolded and larger than males that did not sire extra-pair young (Magrath 1998). Male tarsus length also correlates with extra-pair fertilizations success in blue tits *Parus caeruleus* (Kempenaers et al. 1992). Rather than conveying a cost, therefore, male size appears to enhance the reproductive success of male fairy martins, at least in terms of extra-pair mating success.

Perhaps large size is also an advantage to males when competing for social mates, and large males favour small females, because these small females are more efficient foragers. This would produce the observed pattern of assortative pairing. These smaller females may then produce more sons (as observed) because they are paired to competitively superior males. A number of studies show that females over-produce sons when paired to larger, higher-quality or more attractive mates (Burley 1986, Ellegren et al. 1996, Svensson and Nilsson 1996, Sheldon and Ellegren 1996, Kölliker et al. 1999, Sheldon et al. 1999). Less competitive, small

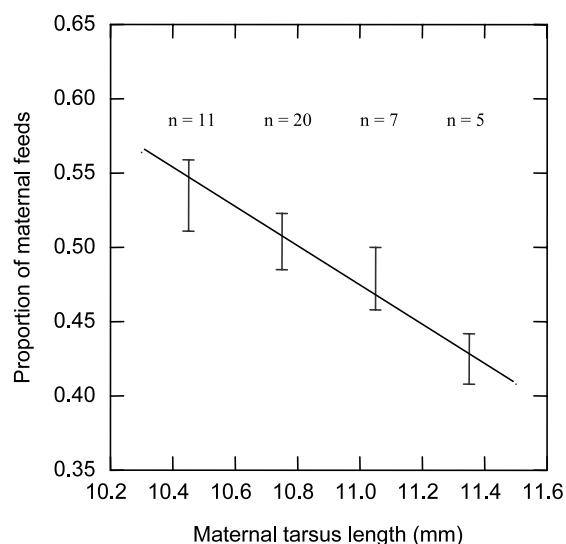


Fig. 2. Proportion of feeding visits by female in pairs of fairy martins in relation to female body size. Line shows predicted proportion of female feeds in relation to tarsus length as derived from logistic regression model ( $\chi^2 = 9.59$ ,  $df = 1$ ,  $P = 0.002$ ; Table 2). Vertical lines depict standard error about mean proportion of female feeds for females in four categories of tarsus length. N values refer to number of pairs in each category.



males would be left to pair with the less favoured large females, and these females may over-produce daughters to avoid producing low quality sons. While this hypothesis is consistent with some of our observations, a strong association between male size and brood sex ratio would be predicted, but this was not evident. Furthermore, offspring produced would be of average size, assuming a genetic component to body size, inherited equally from both parents. Interestingly, this latter problem would be mitigated if body size was more strongly inherited paternally than maternally because the more successful pairings of large males and small females would produce mainly large sons, while the less successful pairings of small males and large females would produce primarily small daughters. However, if this were true, not only would we still predict an association between male size and brood sex ratio, but we would expect this relationship to be stronger than that observed between maternal size and sex ratio, which was clearly not the case. Obviously, more information is required on the heritability and fitness consequences of body size before we can draw any conclusions about how, or even if, the correlation between female size and brood sex ratio is adaptive.

In conclusion, our analyses reveal that the population sex ratio of offspring did not differ from parity in the fairy martin, nor was brood sex-ratio variation explained by any one of a range of environmental or brood-related factors. However, there was a strong relationship between maternal size and brood sex ratio that cannot readily be explained by our current understanding of fairy martin breeding biology. This investigation highlights the need for further studies on sex ratio in a diversity of avian taxa, but also suggests that detailed information about life histories, demographics, and mating behaviour may often be necessary before patterns of sex-ratio variation can be adequately understood.

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